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Physiological tolerances account for range limits and abundance structure in an invasive slug

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Despite the importance of understanding the mechanisms underlying range limits and abundance structure, few studies have sought to do so. Here we use a terrestrial slug species, *Deroceras panormitanum*, that has invaded a remote, largely predator-free, Southern Ocean island as a model system to do so. Across Marion Island, slug density does not conform to an abundant centre distribution. Rather, abundance structure is characterized by patches and gaps. These are associated with this desiccation-sensitive species' preference for biotic and drainage line habitats that share few characteristics except for their high humidity below the vegetation surface. The coastal range margin has a threshold form, rapidly rising from zero to high density. Slugs do not occur where soil-exchangeable Na values are higher than 3000 mg kg⁻¹, and in laboratory experiments, survival is high below this value but negligible above it. Upper elevation range margins are a function of the inability of this species to survive temperatures below an absolute limit of -6.4°C, which is regularly exceeded at 200 m altitude, above which slug density declines to zero. However, the linear decline in density from the coastal peak is probably also a function of a decline in performance or time available for activity. This is probably associated with an altitudinal decline in mean annual soil temperature. These findings support previous predictions made regarding the form of density change when substrate or climatic factors set range limits.

Keywords: abundance structure; desiccation resistance; range margins; salinity tolerance; thermal biology

1. INTRODUCTION

The structure, limits and dynamics of species ranges and the mechanisms underlying them are among the most significant topics in ecology. Indeed, recent work demonstrating that many macroecological patterns can be derived from spatial variation in aggregation (Storch *et al.* 2008), and that human activities are fundamentally altering species ranges (Channell & Lomolino 2000; Parmesan 2006), has re-emphasized their importance. Much theory now exists concerning how range margins might be set by the interaction of ecological and evolutionary processes. Most simply, a population of any given species will persist in an area that is within the reach of individuals given their dispersal ability (or human assistance for introduced species), and where abiotic and biotic conditions are such that birth rates exceed death rates (Brown 1984; Hoffmann & Blows 1994; Holt & Keitt 2000, 2005; Soberón 2007). Even where conditions are not favourable, individuals may still persist owing to a rescue effect, or temporal variation in conditions, frequently making range margins dynamic and diffuse, rather than sharp (Gaston 2003; Crozier 2004). Why populations often do not evolve to overcome local

environmental constraints adds further complexity to the questions of how range margins are set and change (see Hoffmann *et al.* 2003, Alleaume-Benharira *et al.* 2006, Chown & Terblanche 2007, de Mazancourt *et al.* 2008 and Hoffmann & Willi 2008 for discussion).

A large and growing empirical literature exists concerning range limits (see reviews in Brown *et al.* (1996), Gaston (2003) and Parmesan *et al.* (2005)). Nonetheless, several important questions remain unresolved. For example, in the case of the physiological basis of range limits, Gaston (2003) argued that even if it is demonstrated that individuals cannot survive conditions beyond the range edge, this situation might not have arisen primarily owing to the species' physiological tolerances, but because other factors might have limited the species range, with subsequent loss of physiological tolerance. Thus, a fit between physiological tolerance, climatic conditions and the range margin can have more than one interpretation. Recent work has also highlighted several problems with assumptions that are typically made about the role of environmental range limitation (e.g. Davis *et al.* 1998; Austin 2007; Brooker *et al.* 2007; Sax *et al.* 2007; Chown & Gaston 2008). Indeed, only a few studies simultaneously investigate the form of abundance change across a range margin, propose how this change might be linked to a causal environmental factor (or dispersal limitation), demonstrate how the purported mechanism operates at the physiological level, discount the primacy of other, non-physiological factors and provide some indication of what mechanisms

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One contribution of 17 to a Special Issue 'Geographic range limits of species'.

might be constraining evolutionary change to overcome the ecological constraint. Even where much of the evidence has been provided (e.g. Hill & Hodkinson 1992; Crozier 2004; Bird & Hodkinson 2005; Battisti *et al.* 2006; Crozier & Dwyer 2006; Musolin 2007), often the focus remains on one part of the species range margin despite the importance of understanding patterns and processes across the species range (Gaston 2003; Franco *et al.* 2006; Thomas *et al.* 2006; Merrill *et al.* 2008).

Early generalizations concerning the form of abundance structure (see Brown (1984) and Hengeveld (1990) for review) are also now being questioned. Recent empirical work has shown that a unimodal abundance structure is not especially widely supported, owing to much greater complexity of patterns across full ranges or partial components thereof (Brewer & Gaston 2002; Sagarin & Gaines 2002a; McGeoch & Price 2004). However, additional empirical work is required before the generality of these complex abundance structures can be confirmed (Sagarin *et al.* 2006). What is the causal basis of abundance structure also remains largely unanswered empirically (Gaston 2003). Two significant constraints face any study attempting to further work in this area. First, the form of abundance structure must be established before any other work can proceed. Then, appropriate spatial variation in likely causal factors must be investigated and the significance of the factors verified either experimentally or by some independent means. Doing so is by no means trivial (Brewer & Gaston 2003; Klok *et al.* 2003), and more so where an explicit metacommunity framework (Leibold *et al.* 2004) is required.

In this study, we address both major questions, specifically examining the factors responsible for range limits and for variation in abundance structure in a slug species that has invaded an isolated, oceanic island. We chose this system for two major reasons. First, the slug is thought to be having profound impacts on the functioning of the island's terrestrial ecosystem (Smith 2007). Second, owing to the relative simplicity of the island's food web (Burger 1985) and small number of terrestrial species (Gaston *et al.* 2001), teasing out the factors responsible for setting range limits and variation in abundance structure should be relatively straightforward. Therefore, the system should be useful for testing several assumptions that have been made about the form that variation in abundance and environmental factors should take if a causal relationship exists between them (e.g. Caughley *et al.* 1988; Sagarin *et al.* 2006).

2. MATERIAL AND METHODS

(a) *Site and species*

This work was undertaken on subantarctic Marion Island (46°54' S, 37°45' E), which has a cool, wet, windy climate that has shown substantial change over the last 50 years (Le Roux & McGeoch 2008). *Deroceras panormitanum* (Pollonera; Gastropoda: Limacidae) is an air-breathing land slug of Mediterranean origin, which is now virtually cosmopolitan (Holland *et al.* 2007). Although it is known as an invasive in the subantarctic only from Marion Island, it is also invasive on Tristan da Cunha, the Chatham Islands, and in New Zealand (Pugh & Scott 2002), and is also an introduced species in South Africa, with the first records from 1963 (Smith 1992). *D. panormitanum* was first introduced to

Marion Island in the 1970s, probably with fresh produce shipped from South Africa to the island's research station (Smith 1992). It was initially restricted to the vicinity of the research station (Smith 1992), but was later moved to many other areas probably via the wooden containers initially used for the restocking of field huts (Chown *et al.* 2002). It is a generalized detritivore, and is not known to have particular feeding preferences elsewhere in its range (Holland *et al.* 2007) or on Marion Island (J. E. Lee 2008, unpublished data). Southern Ocean island systems have few predators, parasitoids and parasites (Vernon *et al.* 1998), and although the introduced house mouse, *Mus musculus*, is a predator of several invertebrate species on Marion Island (Crafford & Scholtz 1987; Smith *et al.* 2002), no records exist of this species feeding on slugs under any circumstances (Gleeson & van Rensburg 1982; Smith *et al.* 2002). Furthermore, no reports have been made of parasitism or disease in *D. panormitanum* from Marion Island, despite such records being available for other invertebrates on the island (e.g. Chown & Scholtz 1989; Theodorides & Chown 1992; Lee *et al.* 2007).

(b) *Assumptions of the current approach*

In using this invasive species and island system, we explicitly make three key assumptions. First, the abundance structure and range limits in a relatively isolated part of a species range can be used to understand such processes more generally (see Brown (1984), Hengeveld (1990), Gaston (2003) for support for this assumption). Second, the island situations can be used to investigate mechanisms underlying species range and abundance structure (as is frequently done for species on the islands that constitute the UK, and elsewhere e.g. Hodkinson *et al.* 1999; Thomas *et al.* 2001; Gaston & Blackburn 2003; Gaston *et al.* 2006). Third, in this specific instance, dispersal from other populations of the species to the island no longer takes place, and has not taken place at least for the past several decades. Given the very stringent management plan that is presently in place, and the management conditions that have been in operation since the 1990s (details in Chown & Froneman 2008), this latter assumption is defensible.

(c) *Abundance structure and range limits*

During April 2007 and April 2008, surveys to determine the distribution and abundance of *D. panormitanum* were made of much of the coastal and inland habitat of Marion Island using a stratified random sampling approach. The stratification was by habitat type (see Chown & Froneman (2008) for a description thereof) and included biotic, drainage line, mire, saltspray, fernbrake and fellfield habitats. Each time a habitat type was entered, while traversing the coastal plain, and along several altitudinal gradients (appendix S1 in the electronic supplementary material), a sample was taken from at least 10 m from the habitat-type boundary. Each sample consisted of a 0.09 m² quadrat that was searched thoroughly to the soil surface for slugs. If a habitat type was continuous for more than 500 m (at the classification resolution we used several habitats are continuous in this way, e.g. mire, fellfield), additional plots were surveyed until the point that a new habitat type was reached. To confirm the altitudinal limits of the species, areas of suitable habitat were surveyed for an additional 100 m altitude above the highest quadrat at which a slug was found in that area. For each quadrat, slug abundance, latitude, longitude and habitat type were recorded.

Two approaches were adopted for investigating the form of the spatial density variation. First, density data (as slugs m^{-2}) for each quadrat were plotted spatially using ArcGIS (v. 9.1 ESRI, CA, USA), and a natural neighbour algorithm (Sambridge *et al.* 1995) was used to interpolate abundance structure (in the form of density). Then, based on the clear coastal and elevational limits revealed by the former approach, all density data were plotted against altitude to determine the form of their relationship. In particular, the data were inspected for thresholds or gradients of the form predicted by Caughley *et al.* (1988), and the latter confirmed using quantile regression as implemented in Blossom statistical software W2008.04.02 (USGS, Fort Collins, CO, USA; Cade & Richards 2005). To investigate the higher altitude decline in density, the quantile function (0.95) was used with density as the dependent variable. To investigate the lower altitude end of the distribution, it was necessary to consider altitude, as the dependent variable, and to examine the 0.1 quantile.

(d) Environmental correlates

To investigate the proximate correlates of density variation across the island, a generalized non-linear model was built in STATISTICA v. 8 (Statsoft, Tulsa, OK, USA; assuming a Poisson error distribution and using a log link function, corrected for overdispersion). The model included a third-order polynomial for trend surface analysis based on mean-centred latitude and longitude (see Legendre & Legendre 1998) and altitude as continuous predictors, and habitat type as a categorical predictor. The best-fit model was sought using the Akaike information criterion (AIC) and Akaike weights (Johnson & Omland 2004). Because it seemed likely that aspect might also affect slug density, the analysis was repeated including aspect as a categorical factor (see the electronic supplementary material).

Altitude is an indirect environmental variable (Austin 2007), and is a proxy for variation in a variety of other, direct environmental variables. The most notable environmental change with altitude on Marion Island is a decline in temperature, and perhaps an increase in rainfall, although changes in both variables may be nonlinear (Blake 1996; Deere *et al.* 2006; Nyakatia & McGeoch 2008). Owing to the remote nature of most part of the island, temperature data over the full altitudinal transect are available only for the eastern part of the island (Deere *et al.* 2006) and for a small western area (Nyakatia & McGeoch 2008). Here, we examined the eastern dataset over the period 2002–2007, spanning the altitudinal range 0–400 metres above sea level (m.a.s.l.) at 100 m intervals (see the electronic supplementary material).

A sharp edge at the seaward side of the species range (see §3), but high densities at this edge, suggested that a change in substrate quality might be responsible for the range margin. We hypothesized that the most likely driver of this margin, given what is known of slug biology in general (South 1992), would be salinity, especially since during initial surveys it became clear that coastal sites protected from salt spray had relatively high slug densities. To determine the effect of environmental salinity on slug densities, 56 sites on areas that were both sheltered from and exposed to salt spray, and at varying distances from the sea, were surveyed using the methods described earlier, and soil samples were taken at each site. Samples were air dried and exchangeable sodium was quantified (BemLab, Somerset West, South Africa).

A generalized linear model (assuming a Poisson distribution, using a log link function and corrected for overdispersion) was used to investigate the significance of distance and exchangeable Na as continuous predictors of slug density.

We further hypothesized that variation in the density of *D. panormitanum* associated with habitat types, might be related to temperature and humidity conditions characterizing the various habitats for several reasons: (i) poor desiccation resistance of slugs and their strategy of behavioural avoidance of desiccation (South 1992), (ii) the dry conditions typical of exposed sites at the island (despite high rainfall, see Klok & Chown (1998) for discussion), (iii) poor tolerance of low temperatures in molluscs (Ansart & Vernon 2003), and (iv) generalized detritivory in the species. Temperature and humidity were measured using standard techniques both within the vegetation (or just above its surface where cushion plants predominated) and at 1 m above the vegetation, and the difference between the two used as an assessment of the effect of vegetation. The difference, for each variable, was compared among habitat types using a one-way ANOVA (see the electronic supplementary material for details).

(e) Physiological traits

Individuals of *D. panormitanum* were collected daily from Trypot Beach (46°53.09' S, 37°51.61' E) and returned to the laboratory within 2 hours of collection. The slugs were sorted in the laboratory and placed at low densities (15–20) in 250 ml plastic containers. Several physiological traits were investigated using standard methods (e.g. Klok & Chown (1998), Terblanche *et al.* (2005) and Slabber *et al.* (2007), described in full in the electronic supplementary material). Specifically, supercooling point (SCP), lower lethal temperature, desiccation resistance at 100, 76 and 7 per cent RH, salinity tolerance (100, 75, 50 and 0 per cent solution of seawater) and metabolic rate variation with temperature was examined. Animals used in these trials were held at 5°C, 100 per cent RH, 12 L : 12 D, for 8 days prior to the experiments to reduce variation associated with different field conditions. The slugs were held on leaves and litter of *Cotula plumosa* (Asteraceae) on which they often occur in the field. For the metabolic rate and SCP determinations, additional animals were held at 0, 5, 10 and 15°C to investigate acclimation effects on these traits.

(f) Genetic diversity

Although the relationship between evolutionary capacity and variation in genetic markers is not straightforward (Hoffmann *et al.* 2003; Dlugosch & Parker 2008), diminished variation may still indicate an inability for a given population further to evolve. In consequence, we used a neutral marker (mitochondrial COI) to investigate the extent of genetic variation, at least for this locus, in the slug population. Twenty-five slugs from eight localities were sequenced using standard protocols (see Lee *et al.* (2007) and the electronic supplementary material for further information).

3. RESULTS

In total, 1109 quadrats were surveyed around the island and between 2 and 494 m altitude. The abundance frequency distribution was right skewed—most quadrats contained no slugs and the highest density was 344 slugs m^{-2} (figure S1 in the electronic supplementary material). The natural neighbour interpolation revealed

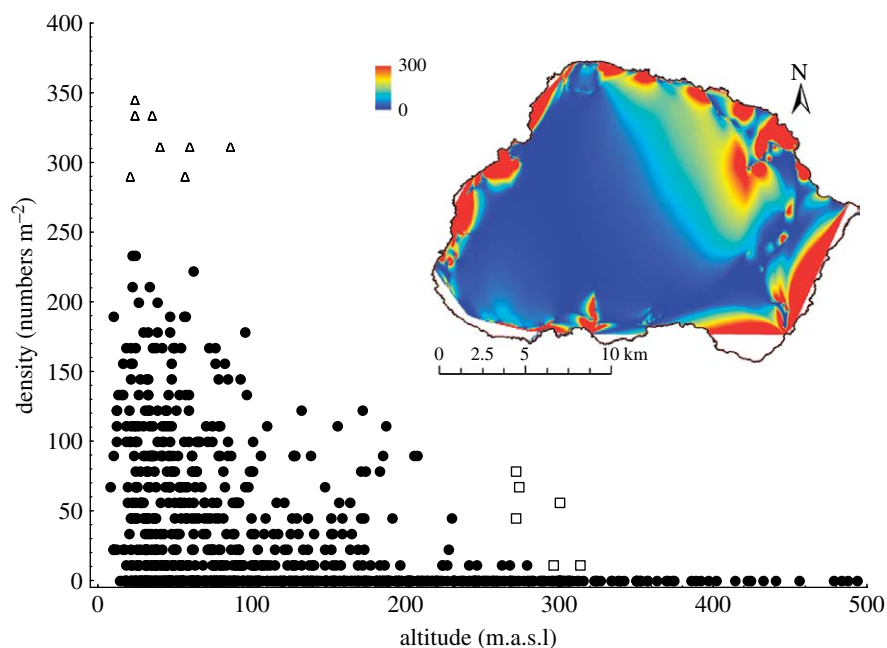


Figure 1. *Deroceras panormitanum* density plotted against altitude for all 1109 quadrats sampled on Marion Island. The open triangles indicate Trypot Beach on the east coast and the open squares the high altitude site above Micked Pickle Cove. The inset shows the natural neighbour interpolation of slug density (numbers m^{-2}) across the island.

a complex abundance structure with patches and gaps (figure 1). Unsurprisingly, the best-fit model for the density data ($\text{AIC} = 203\,364$, $w_i = 0.99$) included all terms in the trend surface third-order polynomial, and also included altitude and habitat type, with the latter variables being highly significant (table S1 in the electronic supplementary material). Abundances were the highest in the biotic and drainage line habitats and low elsewhere (figure 2a). In these latter habitats, aspect was also a significant predictor of density (the best-fit model included all spatial terms, vegetation, altitude and aspect, $\text{AIC} = 203\,517$, $w_i = 0.94$; see table S2 in the electronic supplementary material), with densities being the highest in north and east-facing slopes and flat areas (figure 2b).

At the landscape scale, the coastal gaps often coincided with high elevation ridges reaching the coast, and the patches with biotically influenced vegetation associated with seal and seabird colonies, and also with drainage lines along high elevation ridges. Across the full elevational range sampled, a clear threshold in density occurs on the coast (supported by the 0.1 quantile slope of -0.081), while a gradual decline in density is associated with an increase in elevation (supported by the significantly negative 0.95 quantile slope of -0.364 , $p < 0.0001$). The relatively high density of slugs above 200 m was found mostly at a site above Mixed Pickle Cove on the west coast (figure 1).

Mean annual soil surface temperature declines in a linear fashion with altitude ($r_s = -0.99$, $p < 0.01$), and the number of hours below 0°C likewise increases rapidly with elevation ($r_s = 0.95$, $p < 0.05$). However, absolute minima and maxima and number of hours below -3°C (a critical threshold for the slug, see below) show more complex variation, with 200 m having an exceptionally low absolute minimum and 31 days with temperatures below -3°C over the full period (table 1, figure 3). While temperatures did not decline below -3°C at 300 m, the number of days below this temperature increased again from 400 m

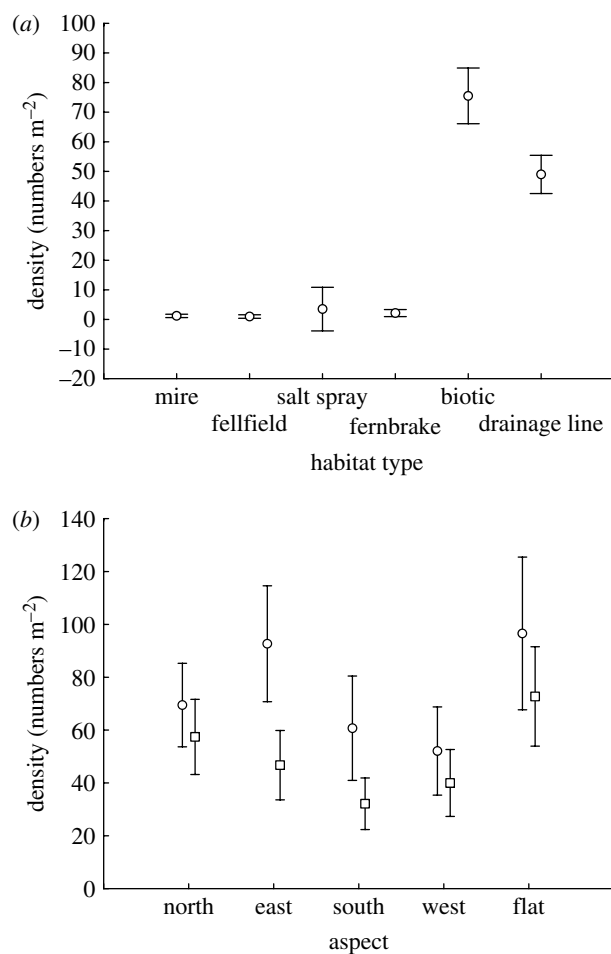


Figure 2. (a) Weighted marginal means ($\pm 95\%$ CI) of slug density in each of the seven habitat types investigated, obtained from a generalized linear model including spatial terms, altitude and habitat. (b) Weighted marginal means ($\pm 95\%$ CI) of slug density in the biotic (circles) and drainage line (squares) habitats, obtained from a generalized linear model including spatial terms, altitude, aspect and the two habitats.

Table 1. Mean, s.d., and minimum and maximum temperatures across an eastern altitudinal transect on Marion Island between 2002 and 2007, and the number of hours and days within that period which were less than or equal to 0°C and less than or equal to -3°C, the mean SCP of *D. panormitanum*. (Rare, light snow cover probably explains the extreme temperatures at 200 m compared with the higher sites that receive more snow.)

altitude (m.a.s.l.)	<i>n</i>	mean (s.d.)	minimum	maximum	hours (days) ≤ 0°C	hours (days) ≤ -3°C
0	38 465	6.31 (2.80)	-1.0	22.5	165 (13)	0
100	38 430	5.53 (3.00)	-0.5	20.0	295 (35)	0
200	38 609	4.96 (3.31)	-10.0	19.0	1397 (141)	396 (31)
300	38 675	4.54 (3.13)	-1.5	19.0	2258 (198)	0
400	37 258	3.84 (3.37)	-8.0	20	4540 (398)	234 (17)

(table 1; and indeed above that altitude to 1000 m, data not shown). Previous recordings by Blake (1996) indicated that precipitation does not decline with altitude, but rather shows an increase to 550 m (from 2873 mm at sea level to 4653 at 550 m).

At the coastal margin, analysis of the additional surveys including estimates of exchangeable sodium revealed that distance to the coast was not a significant explanatory variable ($\chi^2=0.75$, $p=0.39$), although exchangeable sodium was ($\chi^2=33.0$, $p<0.0001$), with density dropping to zero above 3000 mg Na kg⁻¹ (figure 4).

Within the range margins, the biotic and drainage line sites, which had the highest slug densities (figure 2a), did not differ in temperature differential between the 1 m measurement and the vegetation surface or subsurface from the other sites ($F_{4,384}=0.79$, $p=0.53$). By contrast, the high-density habitat types had significantly higher humidities within the vegetation than outside it than did the other sites ($F_{4,384}=26.8$, $p<0.001$; figure S2 in the electronic supplementary material).

The thermal tolerance data indicated that the slugs are unable to survive temperatures lower than -6.4°C, and lower than -2.6 to -3.3°C on average (table 2). Although the treatments had a significant effect on SCP ($F_{2,111}=10.3$, $p<0.001$), as did the positive relationship with mass ($F_{1,111}=28.6$, $p<0.001$), the overall effect size was less than 0.5°C. This was true also of acclimation. Although its effect was significant ($F_{3,116}=7.2$, $p<0.001$), the largest difference among treatments was 0.53°C. Indeed, it seems clear that *D. panormitanum*'s upper elevational range margin coincides closely with the elevation where the lower thermal limits are occasionally exceeded by soil surface temperature minima (figure 3), at least on the eastern half of the island. The metabolic rate data further revealed a linear decline in functioning with temperature ($\log \text{VCO}_2=0.0186 \times \text{temperature} - 1.251$, $t=23.9$, $p<0.0001$, partial correlation=0.77; see figure S3 in the electronic supplementary material). By contrast, salinity tolerance declined in a step-like manner with increasing Na concentration, with zero survival above 3000 mg kg⁻¹ Na ($\chi^2=407.4$, $p<0.0001$; figure 4). High humidity conditions (76% RH) resulted in a mass-corrected desiccation rate of approximately $2.4 \pm 0.32 \text{ mg h}^{-1}$ (LS mean \pm s.e.), whereas at 7 per cent this increased fivefold to $12.5 \pm 0.31 \text{ mg h}^{-1}$ (see figure S4 in the electronic supplementary material).

The mt COI sequence data indicated that a single haplotype characterizes all 25 individuals examined.

Table 2. Mean, minimum and maximum values in °C for SCP following three laboratory treatments and from field fresh individuals. (The lower lethal temperature value is the temperature at which 50% mortality occurred, estimated from a logistic regression, as well as the temperature at which survival declined to zero.)

parameter	<i>n</i>	mean (s.e.)	minimum	maximum
SCP (dry)	47	-3.4 (0.12)	-6.4	-2.2
SCP (wet)	36	-3.0 (0.04)	-3.3	-2.4
SCP (starved)	32	-3.4 (0.04)	-3.8	-3.0
SCP (field)	29	-3.1 (0.05)	-3.8	-2.6
LLT	112	LT50 = -2.6	LT100 = -4.3	

4. DISCUSSION

Despite its restriction to the lower elevations of Marion Island, the abundance structure of *D. panormitanum* does not take the form of a simple unimodal distribution as was once widely thought to be the case (Brown 1984; Hengeveld 1990). Rather, it is characterized by patches of high and gaps of low density. Even over the elevational range taken as a whole (i.e. ignoring other spatial variation), density does not peak in the centre, but rather is the highest close to the coastal margin, declining inland up to approximately 200 m. For an island of this overall, elliptical shape and with a considerable change in elevation, a central peak in abundance might be expected to take a torus-like form, but this was clearly not the case for *D. panormitanum*. Complex abundance structures are now considered the norm rather than the exception, with little evidence for an 'abundant centre distribution' either across entire ranges or partial components thereof (Brewer & Gaston 2002; Sagarin & Gaines 2002b; Gaston 2003; McGeoch & Price 2004; Sagarin *et al.* 2006).

In most continental situations, the mechanisms underlying spatial variation in abundance structure are likely to be complex, including not only physiological tolerances and resource preferences, but also spatial variation in parasitism and predation, dispersal ability and interactions across the metacommunity (e.g. Brewer & Gaston 2002, 2003; Klok *et al.* 2003; and also Leibold *et al.* 2004; de Mazancourt *et al.* 2008). On Marion Island, the scope of interactions between slugs and other species is likely to be small. No predation or parasitism has been recorded, and detritus is an abundant resource in the system owing to the absence of major herbivores (Chown & Froneman 2008). Indeed, the current investigation indicates substantial habitat preference in *D. panormitanum*, for biotic

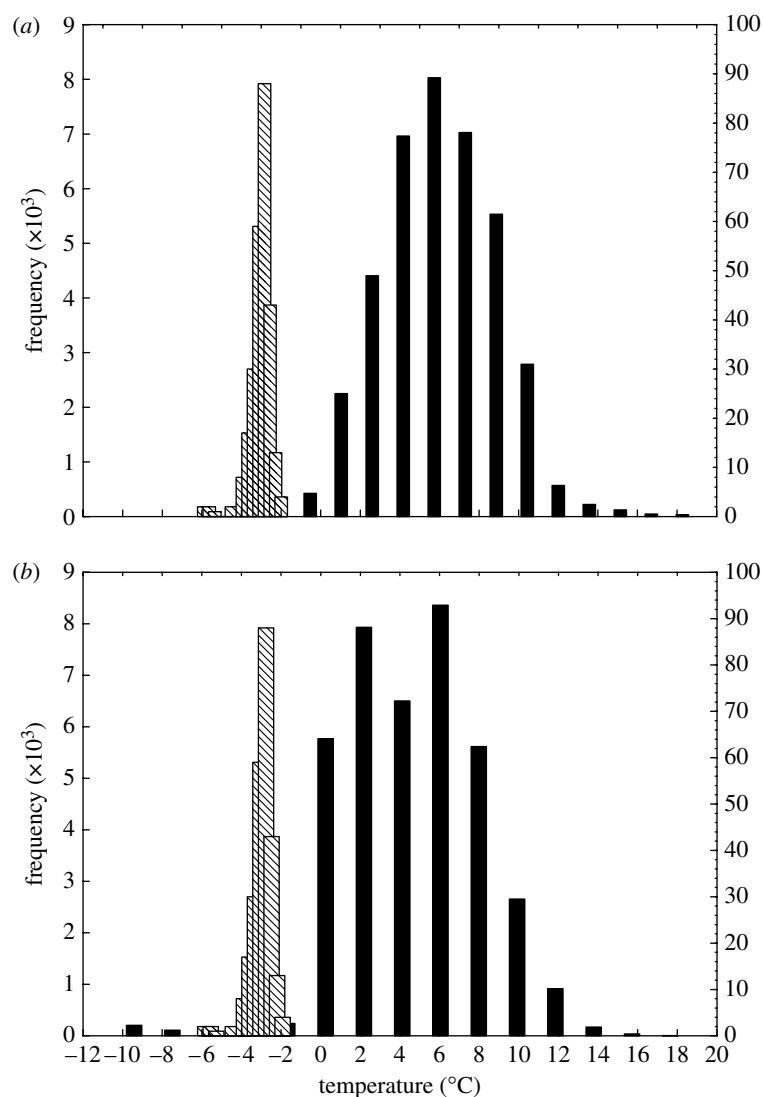


Figure 3. Frequency distributions of soil surface temperature (filled bars) and the supercooling points (SCP) of *D. panormitanum* (hatched bars) at (a) sea level (ca 10 m.a.s.l.) and (b) 200 m.a.s.l. Note that the lowest soil temperatures at 200 m lie beyond the frequency distribution of the SCPs.

and drainage line habitats, which seem to be associated with high humidities in these habitats by comparison with fellfield, mire and fernbrake. The former habitats share few other characteristics, differing substantially in their total nutrient pools, and dominant vascular plants (Poaceae and Asteraceae versus Rosaceae; Chown & Froneman 2008). Moreover, the physiological data indicated that *D. panormitanum* is highly susceptible to desiccation. Indeed, for its size and metabolic rate, it has exceptionally high water loss rates by comparison with other terrestrial invertebrates such as velvet worms and insects (see Klok & Chown (1998) and Clusella-Trullas & Chown (2008) for data and rationale for such a comparison). In consequence, it seems likely that habitat selection, to reduce desiccation which can substantially compromise survival (South 1992), is the major contributor to spatial variation in abundance structure within the limits of this species' range on Marion Island.

Unlike the expectation for most organisms (MacArthur 1972; Brown 1984; Brown *et al.* 1996), in *D. panormitanum* both the coastal and higher elevation range margins appeared to be set by abiotic conditions. On the coastal side, a clear stepped or threshold decline in density was

found overall (supported by the quantile slope close to zero) and substrate salinity appeared to be responsible for this change in density. Individuals of *D. panormitanum* cannot survive direct exposure to more than approximately $3000 \text{ mg kg}^{-1} \text{ Na}$, and as soon as this value is exceeded in the soil, substrate density declines to zero irrespective of the distance from the sea, as indicated by the additional survey data. In other words, where coastal sites are highly protected and include the biotic habitat they form favourable sites, such as Trypot Beach (figure 1). This threshold-like change in density associated with a change in substrate quality (in this case Na content) provides support for Caughley *et al.*'s (1988) contention that changes in substrate should lead to a stepped range margin.

Although the partial nature of this study (i.e. not over the full distribution of the species), and the relatively simple nature of the food web on the island (Burger 1985; Gaston *et al.* 2001) might account for the unimportance of biotic factors in setting the lower elevation range limit, other studies have reached similar conclusions concerning the significance of abiotic range limitation (see Merrill *et al.* (2008) for an example for a lower elevational limit,

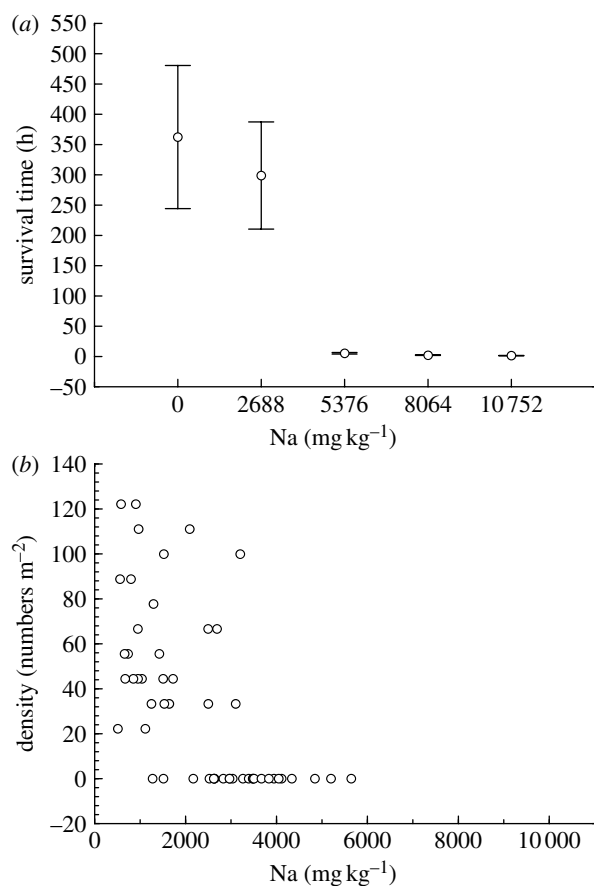


Figure 4. (a) Mean ($\pm 95\%$ CI) survival of *D. panormitanum* exposed to different seawater concentrations (converted to Na equivalents in mg kg⁻¹). (b) *Deroceras panormitanum* density in 56 coastal quadrats plotted against soil-exchangeable Na concentration.

and Mercader & Scriber (2008) for the southern range limit of a northern butterfly species). As with many other biological generalizations, those concerning the significance of abiotic versus biotic range limitation of species' range margins may have several exceptions.

Having said that, it seems clear that the upper elevational limit to the *D. panormitanum* population on Marion Island is set by temperature. The physiological investigations indicated that *D. panormitanum* is incapable of surviving below a mean of -3°C and a minimum of -6.4°C . These temperatures are exceeded at 200 m, albeit on an infrequent basis. Nonetheless, as indicated by the SCP and soil surface temperature frequency distributions, these infrequent low-temperature events would be sufficient to eliminate the entire population. At a few sites above 200 m, slug densities as high as 50–80 slugs m⁻² were found. If occasional extreme temperatures are responsible for setting the range margin, then temporal variation in its edge might be expected (e.g. Crozier 2003, 2004), a plausible expectation given mean slug locomotion rates of 5.0–7.9 m h⁻¹ (on a flat surface) at temperatures between 0 and 5°C (Chown 2006, unpublished data). Moreover, six of these sites were restricted to the west coast of Marion Island, just above Mixed Pickle Cove. Recent work has shown that this area has both milder winter soil surface temperatures and cooler summer ones than the eastern part of the island (Nyakatia & McGeoch 2008), which may account for the persistence of slugs in reasonable densities at 300 m.

Indeed, the existence of a thermal refuge beyond the usual limits of the species supports the idea that low temperature is a limiting factor (see Gaston (2003) for additional examples). Of course, it might be argued that the unavailability of habitats might also have contributed to range limitation given the change in habitat type with elevation on the island (Chown & Froneman 2008). However, several drainage line and biotic sites (associated with burrowing seabirds) above 200 m were examined and found to be free of slugs.

While the edge of the range at the higher elevations does seem to be set by an absolute temperature limit, the decline in density with elevation is more difficult to explain. Caughley *et al.* (1988) suggested that if density shows a ramp-like decline, and 'well-being' a similar change, climate is probably the factor affecting a species boundary. Here, density certainly showed a clear linear decline as demonstrated by the quantile regression. Similarly, mean annual temperature declines and the number of days below 0°C increases rapidly with elevation. Based on the decline in standard metabolic rate with temperature, and assuming that metabolic rate can be used as a proxy for performance or well-being (see discussion in Chown & Gaston 1999), it seems likely that the decline in density may be a consequence of a decline in performance, or, perhaps as a consequence, time available for activity, as elevation increases. Few other reasons to explain the decline in abundance with elevation seem plausible, especially since precipitation does not decline with elevation (as far as is known), habitats remain available, and predation is non-existent. The only other potential explanation for the decline in density might be an indirect interaction with the major indigenous detritivore on the island, caterpillars of the flightless moth *Pringleophaga marioni* (Smith 2007), owing to altitudinal variation in predation pressure by mice on this species (Phiri *et al.* in press). However, detritus does not seem to be a limiting factor on Marion Island given that so much of it ends up being transformed to peat (Smith 2007). In consequence, the decline in temperature with elevation probably accounts for the decline in slug density.

In conclusion, it appears that the lower and upper elevational range margins of *D. panormitanum* are set by its physiological tolerances, of salinity and low temperature, respectively. While it might be argued that some other factor has set the species' range margins, and tolerances have subsequently evolved to reflect the situation (Gaston 2003), the absence of other limiting factors make such a supposition implausible. Moreover, although the mt COI neutral marker is unlikely to reflect fully the evolutionary potential of this island population (Dlugosch & Parker 2008), the single haplotype found does suggest that it has passed through a considerable bottleneck. Only further work will reveal the extent to which this may have been limiting and may be limiting in the future. The latter is especially significant since, although current and forecast climate change at the island include increases in mean annual temperature, these are being accompanied by increases in the frequency of freeze-thaw events owing to more common clear sky conditions (Chown & Froneman 2008). Thus, the future may well see higher slug densities over a narrower elevational range than is presently the case.

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